

STRATEGIES OF GALL FORMATION IN
PEMPHIGUS APHIDS^{1, 2}

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Introduction

This is a study of the various aspects of the strategies of gall formation by two species of aphids which form galls on the leaves and petioles of the Eastern Cottonwood, *Populus deltoides*. *Pemphigus* galls are initiated when a young stem mother or fundatrix (the name for the first parthenogenetic generation after the sexual generation) begins feeding on the newly emerging leaves of *Populus*. On Long Island, the two common gall-forming species on cottonwood are *Pemphigus populicaulis* Fitch and *P. populitransversus* Riley. These induce "oblique" and "transverse" galls, respectively. The *oblique gall* is formed by a swelling and twisting of the leaf at the point where the blade meets the petiole. The *transverse gall*, by contrast, is formed entirely on the leaf petiole. In each case, feeding by the fundatrix induces changes in the growth of the plant tissue, resulting in a chamber enclosing her. The parthenogenetic offspring of the mature fundatrix usually remain within the gall until after a final molt that, in all cases, results in winged individuals. These winged forms (alate fundatrigeniae, called "alates" for short in this paper) migrate to the roots of a secondary host plant (members of the Cruciferae or Compositae). After one or more parthenogenetic generations on the secondary host, winged forms ("sexuparae") are produced that return to the primary host (*Populus*) and give birth parthenogenetically to sexual forms. Each fertilized female deposits, in cracks in the bark of the tree, a single egg which in turn develops into a fundatrix, completing the life cycle (Harper 1959). The exact timing of these life history stages for *P. populicaulis* and *P. populitransversus* will be discussed later in this paper.

Initiation of *Pemphigus* galls has been observed only on young, newly unfolding leaves. *P. deltoides* produces leaves continuously throughout the summer; early leaves are preformed in the winter bud and morphologically distinct late leaves are formed from leaf primordia after the expansion of the early leaves (Kozlowski 1971). As a result, feeding sites for young fundatrices are continuously available from spring until late summer. However, once the fundatrix initiates a gall, it does not appear to change its feeding site.

For purposes of this paper, I shall define "gall position" as one plus the number of leaves on a shoot preceding (older than) the leaf bearing the gall.

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For example, if the gall position is "6," then the gall is located on the sixth leaf of the shoot, counting from the base of the shoot.

Obviously, the proximal causes of a given gall position are the time the fundatrix nymph emerges and initiates the gall, the time of bud break of the shoot, and the subsequent rate of leaf expansion of the shoot. The ultimate causes of gall position, that is, the selective pressures affecting the timing of gall initiation, are discussed in this paper.

Whitham (1974) first considered the adaptive significance of the position of *Pemphigus* galls on cottonwoods. He showed that galls sharing the same leaf were generally smaller than single galls, and argued that the aphids were resource (sap) limited. He found a significant correlation of gall size with leaf size for oblique and transverse galls, and also showed that galls of both species are found on larger-than-average leaves. He suggested that the obliques may achieve this through the timing of gall formation and the transverse through the "choice" of longer shoots bearing larger leaves.

My preliminary observations on one tree showed that of 129 oblique galls, 97 (75.2%, with 95% confidence levels 66.5–82.8%) were found on the largest leaf of their shoot. However, of 154 transverse galls, only 38 were found on the largest leaf (24.7%, limits 19.1–33.0%). The correlation of leaf length with gall diameter was 0.87 ($n = 129$) for oblique galls and 0.39 ($n = 154$) for transverse galls. This suggested that, to the extent that fitness is related to gall size, leaf length might influence the success of transverse galls less than that of oblique galls.

In this paper a dimorphism in gall position of *P. populitransversus* is demonstrated. Then, the possible factors affecting relative success of these galls are determined with the goal of discovering whether there is differential fitness at different gall positions. Finally, for both *P. populitransversus* and *P. populicaulis*, position is analyzed as a possible response to such selection pressures.

Materials and Methods

Observations and collections were made from cottonwood trees in the vicinity of Stony Brook, Long Island, starting in early May, 1975. Measurements of the cottonwoods were made in the field and galls were removed, tagged, and placed in jars of alcohol. *Populus* measurements included tree height and for shoot samples, the number of leaves on the shoot, gall position, position of the largest leaf, petiole lengths, and leaf lengths. In the laboratory, each gall was measured and its aphid population censused under a dissecting microscope. The numbers of winged forms and individuals in three arbitrarily chosen size classes of nymphs were recorded for all galls. Galls that showed signs of predation or other disturbances were not used for this study.

Relative reproductive success of different fundatrices was estimated by censuses of galls in which some winged forms had developed. This seems to be a reasonable estimate of the reproductive potential of a gall for the season. In a study of six species of *Pemphigus* in Alberta, including *P. populicaulis* and *P. populitransversus*, Harper (1959) found a correlation of 0.99 between the *average number of aphids* emerging from a gall for a given species over the summer and the *average population counts in galls* in a separate sample of that species. I will also assume that, within a species, differences in population counts among galls reflect differences in the number of migrants that could be expected from the galls over the summer.

Dimorphism in the Timing of Gall Initiation in *P. populitransversus*

Gall initiation by *Pemphigus populitransversus* was found to occur at two clearly separate times during the summer of 1975. Gall initiation is first detected as a slight swelling and bending of the petiole at the point where a fundatrix nymph has begun feeding. In this early stage, the young fundatrix is not enclosed and appears as a small black spot in the pocket formed by the swelling and bending of the petiole. Transverse galls first began forming, along with oblique galls, around May 15 on cottonwoods in the vicinity of Stony Brook. At this time, the early leaves of the tree were expanding and provided suitable sites for gall initiation. The trees were checked carefully on successive days, and after two or three days, there was no further gall initiation. Then, on June 15, more transverse galls began forming on the newly formed late leaves. This dimorphism in the timing of gall initiation resulted in a set of galls on the early leaves and a set of galls on the late leaves of the shoots. The early transverse galls had an average position of $6.2 \pm .39$ ($n = 48$), over several trees, while the average position of the late galls was $16.2 \pm .35$ ($n = 85$).

A dimorphism in gall shape, life history, and aphid morphology has been described for this species by Senner and Sokal (1974). The morph they refer to as "*elongate*" produces galls that are more elongate in shape than those of the other morph called "*globular*." The question immediately arose whether the presence of early and late transverse galls was related to the globular-elongate dimorphism. An analysis of the early and late transverse galls confirms the suspected relationship (Table 1). The late galls are larger than the early galls, and more spherical, as shown by the ratios of gall dimensions. The values in Table 1 resemble those of the sample from West Point, Georgia, shown in Table 3 of Senner and Sokal (1974). The early and late galls were significantly different for each character. Corroborating tests were run following methods developed by Senner and Sokal (1974). The gall dimensions and their ratios split a mixed sample of 71 galls into early and

Table 1. Means of gall characters for 39 early and 31 late transverse galls in Stony Brook, New York, 1975.

Gall character	Early transverse	Late transverse	F_s
Length	10.9	14.7	38.9
Width	7.5	14.3	19.4
Depth	8.0	13.4	12.4
Length/width	1.46	1.03	77.2
Length/depth	1.38	1.11	20.5

Note: Measurements are in millimeters. F_s is the sample F -statistic testing differences between the means. All values of F_s are significant at $P < 0.001$.

late classes fairly well. Only two galls would be misclassified by time of gall formation when the sample was split according to gall depth and only 4 galls would be so misclassified on the basis of length/width ratio. It is highly probable that the early and late galls correspond to the elongate and globular morphs, respectively.

Population Sizes in Globular and Elongate Galls

Senner and Sokal (1974) found that globular galls had larger within-gall population sizes than elongate galls. Table 2 summarizes the data on population size for several trees on Long Island. In a pooled sample from several trees, the population size of globular galls was higher than that of elongate galls; the average population size of globular galls was 377.6 ± 19.2 ($n = 60$) compared with 290.9 ± 13.6 ($n = 52$) for elongate galls, for trees on which both types of galls were present. These values were significantly different ($F_s = 10.4 > F_{.005(1,111)}$). For individual trees, the results were somewhat variable (Table 2). The difference in population size between elongate and globular morphs was significant for both tree 4 and tree 8 ($F_s = 9.8 > F_{.005(1,46)}$, $F_s = 7.6 > F_{.025(1,21)}$). For tree 3, the difference in population sizes of the two morphs was not significant ($F_s = .128 < F_{.90(1,24)}$). Thus, average population size is somewhat variable among trees for each morph, but in general, stem mothers of globular galls produce more offspring than those of elongate galls.

Table 2. Mean population size (\pm standard error) of globular and elongate galls for different trees in Stony Brook, New York, 1975.

	Tree 3	Tree 4	Tree 8
Globular	376 \pm 46.3 (14)	409 \pm 29.0 (29)	454 \pm 37.3 (12)
Elongate	357 \pm 26.4 (11)	237 \pm 20.1 (18)	294 \pm 19.1 (10)

Note: Sample sizes (number of galls) in parentheses.

Table 3. Analysis of covariance of population sizes of globular galls on characteristics of the galls, and correlation matrix for these variables.

Source of variation	Sum of squares	df	Mean squares	F_s
Corrected total	1638165.15	73		
Adjusted treatment	212100.79	2	106150.40	13.53***
Regression	1073545.41	6	178924.24	22.82***
Error	509518.67	65	7838.75	
Regression homogeneity	111766.55	12	9313.88	1.24ns
Error for regression homogeneity	397752.13	53	7504.76	

Partial regression coefficients						Adjusted treatment means		
GL	GW	GLP	LAG	GPL	GLL	Tree number		
23.0	30.6	-6.5	4.0	-20.1	-.7	2	3	4
						314.5	478.7	396.3

Correlation matrix							Population size
	GL	GW	GLP	LAG	GPL	GLL	
GL		.618	.008	-.217	-.498	.000	.612
GW			.000	.116	-.327	.200	.684
GLP				.008	.000	.326	-.097
LAG					.000	.299	.131
GPL						.000	-.284
GLL							.009

Note: Treatments are differences among three trees. Gall characteristics used as covariates are: GL—gall length, GW—gall width, GP—gall position, LAG—number of leaves after gall position, GPL—number of galls per leaf, GLL—length of leaf bearing the gall. Significance values are symbolized by ***— $P \leq .001$, **— $.001 P \leq .01$, *— $.01 P \leq .05$, ns— $P > .05$. All correlation coefficients significant at $P \leq .01$ are in italics.

What factors account for the variation in population size among galls within each morph? Can factors relating to the difference in gall position of the two morphs account for the greater population sizes of the globular galls? Also, is there evidence of competition between galls? Such evidence would suggest some limiting factor on population size. I shall address these questions in turn.

The population size of globular galls was used as the dependent variable in an analysis of covariance (Table 3). Gall length, gall width, gall position, the number of leaves after (distal to) the gall position, the number of galls per leaf, and the length of the gall-bearing leaf were used as covariates and the 3 trees sampled served as treatments. The regression was significant and homogeneous over trees. However, the adjusted treatment means were sig-

nificantly different ($F_s = 13.5 > F_{.001(2,65)}$); therefore, the regression does not completely account for the variation in population size among trees.

The partial regression coefficients for gall length, gall width and gall position were significant ($F_s = 19.8 > F_{.001(1,65)}$, $F_s = 23.9 > F_{.001(1,65)}$, and $F_s = 3.86 > F_{.05(1,65)}$, respectively). As noted earlier, population size increased with gall dimensions. However, it decreased with position. Age of the gall may be responsible for this effect, since galls with lower positions will be slightly older and hence more populated than those at higher positions.

There seems to be some competition among galls on the same leaf, as suggested by the significant negative correlation of number of galls per leaf with gall length and gall width, and the negative correlation of number of galls per leaf with population size (significant at $P < 0.025$). The effect of the number of galls on a given leaf or shoot on population size in the galls seems to be realized through the effect of number of galls on gall dimensions.

For tree 2 alone, competition was tested between galls on the same shoot. The number of galls per shoot was seen to increase with the number of leaves on the shoot ($r = .60$, $n = 31$). The regression of population size on the number of galls per shoot, holding the number of leaves constant, was also significantly negative ($F_s = 8.4 > F_{.001(2,65)}$). There would appear to be competition for resources among globular galls on the same shoot.

Gall leaf length was found to increase with gall position; that is, leaves were larger toward the tip of the shoot. However, the length of the leaf did not seem to be important to the success of the gall. Gall leaf length had no significant correlation with population size, or with gall dimensions. Thus, larger populations are found in larger galls and in earlier positions, but this is not related to leaf size.

A similar analysis of covariance was performed for three trees with elongate galls (Table 4). The regression is significant and, in this case, it does account for the difference in the average population sizes of the three trees, since the adjusted treatment means were not significantly different ($F_s = 2.98 < F_{.10(2,39)}$).

Again, gall dimensions correlate highly with population size in the gall, but only the partial regression coefficient on gall width was significant ($F_s = 4.33 > F_{.05(1,39)}$). Gall leaf length, as in the case of globular galls, increases with gall leaf position and does not show a significant correlation with population size or gall dimensions. However, in contrast to the globular case, the gall position correlated positively with population size. To investigate further any effect due to variation in leaf length with position, population size was regressed on gall position, holding gall leaf length constant. This regression was significant ($F_s = 5.37 > F_{.05(1,40)}$). Therefore, in elongate galls, there must be some factor other than leaf size relating to gall position that affects population size.

Table 4. Analysis of covariance of population sizes of elongate galls on characteristics of the galls, and correlation matrix for these variables.

Source of variation	Sum of squares	df	Mean squares	F_s
Corrected total	427501.48	47		
Adjusted treatment	31698.23	2	15849.14	2.98ns
Regression	121292.59	6	20215.43	3.80**
Error	207382.82	39	5317.51	
Regression homogeneity	55584.99	12	4632.08	.82ns
Error for regression homogeneity	151797.83	27	5622.14	

Partial regression coefficients						Adjusted treatment means		
GL	GW	GLP	LAG	GPS	GLL	Tree number		
10.4	33.3	4.5	-1.9	11.1	-.60	3	4	8
						329.2	285.5	228.1

Correlation matrix							
	GL	GW	GLP	LAG	GPS	GLL	Population size
GL		.445	.253	.110	-.198	.156	.430
GW			.009	.144	-.181	.063	.462
GLP				-.298	.150	.528	.462
LAG					.496	.455	-.170
GPS						.494	.423
GLL							.276

Note: See Table 3.

For elongate galls, competition was examined in terms of galls on the same shoot. Surprisingly, the number of galls per shoot correlated positively with population size within a single tree. The number of galls per shoot correlated with shoot length ($r = .496$, $n = 48$). Longer shoots produce numerous and more populated galls for unknown reasons.

To find the causes of the differences in the average population sizes of globular and elongate galls, these morphs were used as treatments in an analysis of covariance (Table 5) with gall length, gall width, gall leaf length, and the number of leaves after the gall as covariates. The two treatments were significantly different for each of these variables. The treatment means of populations sizes were 378 ± 19.2 for globular and 291 ± 13.6 for elongate galls.

As expected, the partial regression coefficients for gall length and gall width were significant ($F_s = 8.7 > F_{.005(1,128)}$, $F_s = 12.0 > F_{.001(1,128)}$). These gall dimensions account for the differences in population size of the two

Table 5. Analysis of covariance of population sizes between globular and elongate galls on characteristics of the galls, and correlation matrix for these variables.

Source of variation	Sum of squares	df	Mean squares	F_s
Corrected total	2599665.20	133		
Adjusted treatment	243.97	1	243.97	.026ns
Regression	1096649.72	4	274162.43	28.86***
Error	1215984.13	128	9499.87	
Regression homogeneity	63056.38	4	1574.10	1.70ns
Error for regression homogeneity	1152927.75	124	9297.80	

Partial regression coefficients				Adjusted treatment means	
GL	GW	LAG	GLL	Globular	Elongate
15.5	26.9	.24	2.3	352.25	356.24

Correlation matrix					
	GL	GW	LAG	GLL	Population Size
GL		<i>.580</i>	-.020	.140	.612
GW			-.164	.313	.676
LAG				.003	-.064
GLL					.240

Note: Treatments are differences between morphs. Gall characteristics used as covariates are: GL—gall length, GW—gall width, GLL—length of leaf bearing the gall, and LAG—number of leaves after the gall position. ***— $P \leq .001$, **— $.001 P \leq .01$, *— $.01 P \leq .05$, ns— $P > .05$. Correlation coefficients significant at $P \leq .01$ are in italics.

morphs, since there was no significant difference between the adjusted treatment means ($F_s = .026 < F_{.05(1,128)}$).

Within tree number 8, the correlation of gall leaf length and population size, for both morphs, was .560 ($n = 20$). However, overall, the correlation of leaf length with population size (.240) and gall dimensions (.140, .313) was low, and within each morph, gall leaf length did not account for the variation in population size. Therefore, it seemed useful to try another variable that might explain gall size and the relationship of gall position to population size in the elongate morph.

Petiole length and width were tried as variables that might affect gall dimensions. Since transverse galls grow on petioles, the size of the latter might be more closely related to gall dimensions than leaf length. For a new pooled collection of 9 globular and 10 elongate galls from a single tree, petiole width explained 78% of the variance in gall width ($F_s = 63.3 > F_{.001(1,18)}$), and petiole length explained 41% of the variance in gall length ($F_s = 12.3 > F_{.005(1,18)}$). Petiole length and width, then, are better indicators of gall dimensions than gall leaf length for transverse galls.

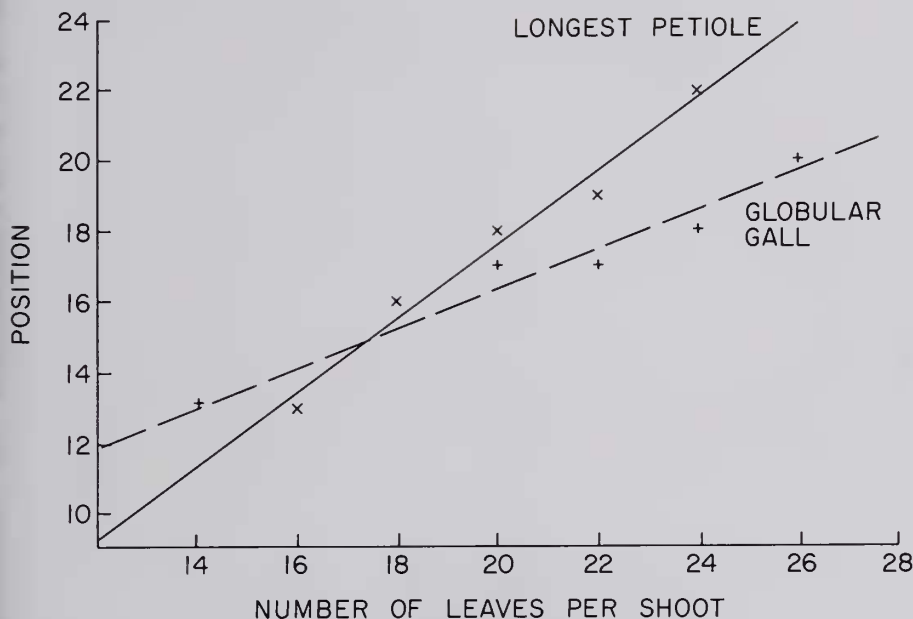


Fig. 1. Position of globular gall (crosses and dashed line) and position of the longest petiole (\times 's and solid line) on the total number of leaves on the shoot. The lines represent significant least squares regression lines. The ordinate is position and the abscissa is total number of leaves. Samples based on tree 2, Stony Brook, New York, 1975. Note that for most shoot sizes the position of globular galls is earlier than that of maximal petiole size.

In this new sample, gall length of the two morphs was not significantly different ($F_s = .5 < F_{.05(1,18)}$), but width of the globular morph was significantly greater than that of the elongate morph ($F_s = 14.7 > F_{.005(1,18)}$). Petiole width for leaves with globular galls was $4.5 \pm .36$ mm and for leaves with elongate galls was $3.1 \pm .22$ mm. My field observations suggest that this difference in width is not due to the presence of the galls on the petioles; measurements of many late and early leaf petioles without galls showed that petiole width of late leaves was rarely as low as 3.0 mm, which was the usual width of early petioles. This difference in petiole width between early and late leaves may indirectly account for the general difference in population size of the two morphs through its effect on gall width. An analysis of covariance was carried out with gall width as the dependent variable, globular and elongate as treatments, and petiole width as a covariate. The regression, controlling for petiole width, was significant ($F_s = 52.4 > F_{.001(2,17)}$). Thus, although petiole width does explain 78% of the variance in gall width for elongate and globular galls taken together, other (possibly genetic) determinants of the differences in gall width of the morphs remain.

In summary, the greater population sizes of globular galls are partly attributable to the greater petiole widths of the late leaves on which these

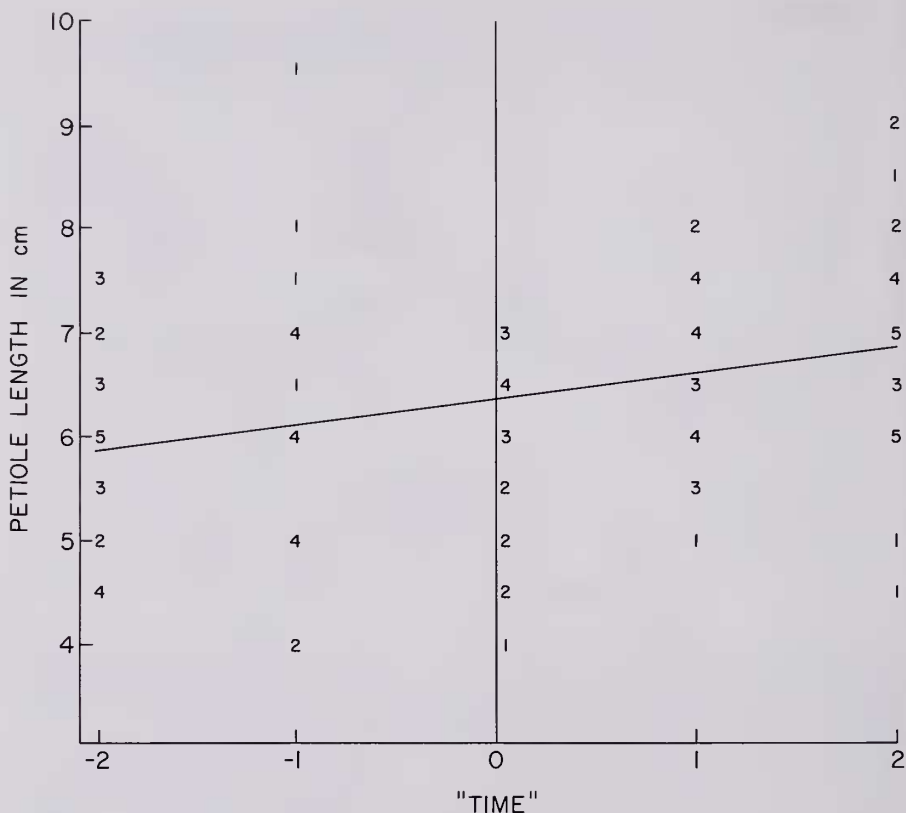


Fig. 2. Regression of petiole length on gall position, holding the total number of leaves constant ($P < .05$). Numbers of graph indicate number of times a given point occurs. The ordinate is petiole length (cm) and the abscissa is "time" (deviation of gall position from regression on total number of leaves per shoot). Sample is made up of globular galls taken from tree 2, Stony Brook, New York, 1975.

galls are found, relative to the petiole widths of the early leaves, which are the sites of the elongate galls.

Position of Globular Galls among the Late Leaves

Position of globular galls, as expected, increases with the total number of leaves on the shoot (Figure 1). Any given time of gall initiation will result in a later position on faster than on slower growing shoots, because the faster shoots will have produced more leaves in the same amount of time. Although population size of a gall did not correlate with gall position, it may correlate with time of gall initiation, which would suggest selective pressure for earlier or later gall initiation. A regression of population size on gall position, controlling for the number of leaves per shoot relates population

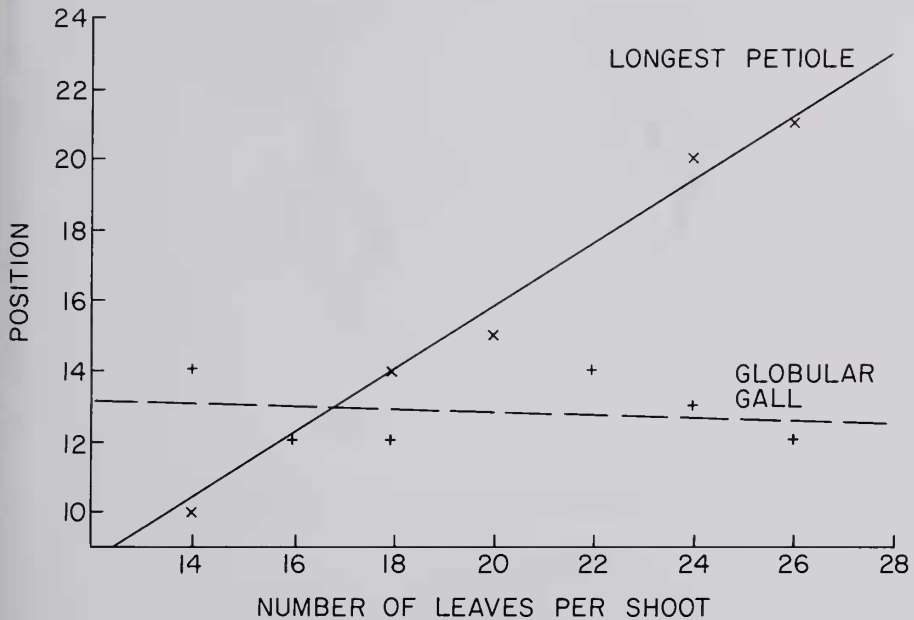


Fig. 3. Globular gall position (+'s and dashed line) and longest petiole position (x's and solid line) on the total number of leaves on the shoot. The solid line represents a significant regression line. Ordinate: position; Abscissa: total number of leaves. Samples are from tree 8, Stony Brook, New York, 1975.

size to time; however, this regression was not significant, so population size is not dependent on time in the data from tree 2.

Since petiole length has been shown to correlate with gall length, I also investigated the possible relationship of position of globular galls with the variation in petiole size of late leaves. Does the position of globular galls maximize petiole size among late leaves? For tree 2, petiole length was regressed on leaf position, holding the total number of leaves constant (Figure 2). Petiole length significantly increased with time, suggesting that later gall initiation may imply an increased population size through the effect of petiole length on gall length. The relationship of the actual positions of globular galls to petiole size is shown in Figure 1. For most shoot sizes, the globular galls appear earlier than the leaf with the longest petiole. The results were similar for another tree (8), as shown in Figure 3. There is no evidence, then, that the globular galls were positioned as an adaption to maximal petiole length among the late leaves.

Positions of Elongate and Oblique Galls among the Early Leaves

For elongate galls alone, petiole length explains 62% of the variation in gall length ($F_s = 17.9 > F_{.001(1,11)}$). Gall leaf length, on the other hand, does

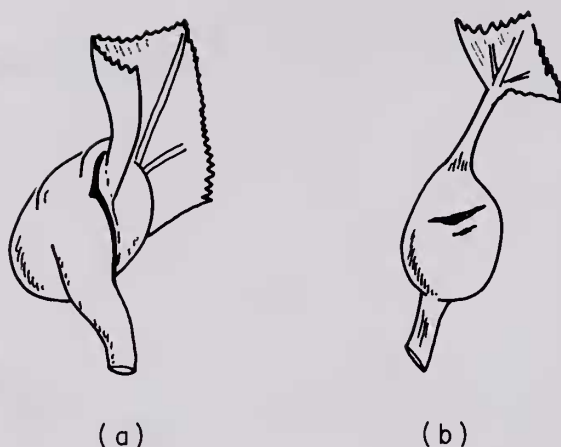


Fig. 4. *Pemphigus* galls. (a) A "typical" gall of *P. populicaulis* ("oblique"). (b) A "typical" gall of *P. populitransversus* ("transverse"). Drawings by Lorenz Rhomberg.

not have a significant correlation with gall length ($r = .156$, $n = 48$). Since gall length was found to correlate highly with population size ($r = .50$, $n = 25$), for tree 4, it might be expected that there would be selection for timing of gall initiation such that the resultant position of the gall provided a larger petiole, on the average. Such selection would be possible if petiole length can be predicted by timing of gall initiation. By contrast, oblique gall diameter correlates more highly with leaf length ($r = .874$, $n = 25$) than with petiole length ($r = .209$, $n = 25$); and gall position might similarly reflect a prediction of leaf size through timing. The reasons for the differences in correlations are clear, since elongate galls are formed on leaf petioles while oblique galls are formed by a twisting together of the base of the leaf blade (Figure 4).

The relative and absolute positions of oblique and elongate galls are not constant from tree to tree (Table 6). Trees 1 and 4 each show elongate galls significantly earlier in position than oblique galls. Tree 3 showed the same trend but the difference was not significant.

Table 6. Mean (\pm standard errors) of oblique and elongate galls of different trees sampled in Stony Brook, New York, 1975.

	Oblique	N	Elongate	N	F_s
Tree number					
1	7.17 \pm .44	15	5.59 \pm .38	22	12.3***
3	8.80 \pm .20	109	8.30 \pm .20	98	3.21ns
4	7.45 \pm .37	21	5.21 \pm .55	19	12.0***
5	6.70 \pm .38	25	—	—	—

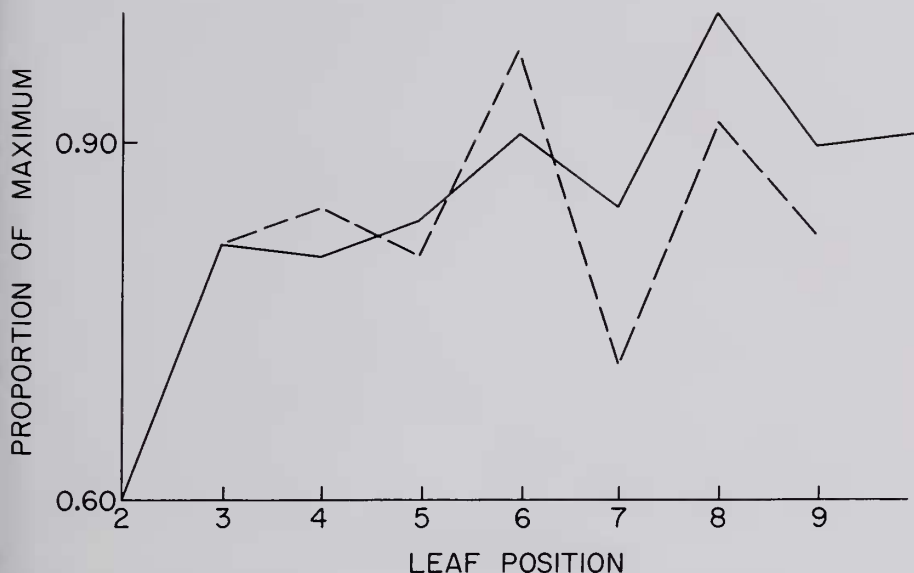


Fig. 5. Leaf length as a proportion of maximum length (solid line) and petiole length as a proportion of maximum length (dashed line) on leaf position. Ordinate: proportion of maximum length; Abscissa: leaf position. Data are for tree 1, Stony Brook, New York, 1975.

For a more detailed examination of the shoots on tree 1 we turn to Figure 5. Only shoots without galls having 9, 10, or 11 early leaves were considered to limit the variability of patterns of leaf or petiole size due to variation in the number of early leaves of the shoots. The abscissa gives the leaf position. The ordinate is the ratio of the length for a given position on the shoot to the maximum length for the shoot. The solid line shows the average proportion of maximum leaf length (length divided by the length of the largest leaf on the shoot) and the dashed line shows the average proportion of maximum petiole length for each position on these shoots. The average petiole length at position 6, the first peak, was 7.92, and at position 8, the second peak, was 7.08. Because of the small sample size ($n = 6$) for each group, these differences are only suggestive ($P = .08$). Leaf length follows the reverse pattern with the average at position 8 (12.1), greater than that of position 6 (10.7) ($F_s = 4.25 > F_{.08(1,10)}$). Again this is only suggestive, but it appears that the position with the greatest average petiole length is before the position with the greatest average leaf length for this tree. Another expression of this difference is that for shoots without galls on tree 1, the average position of the longest leaf, 7.6, was significantly greater than the average position of the longest petiole, 6.1 ($F_s = 30.8 > F_{.001(1,30)}$).

Is this difference reflected in the positions of oblique and elongate galls? The frequency distributions of elongate and oblique gall positions for tree

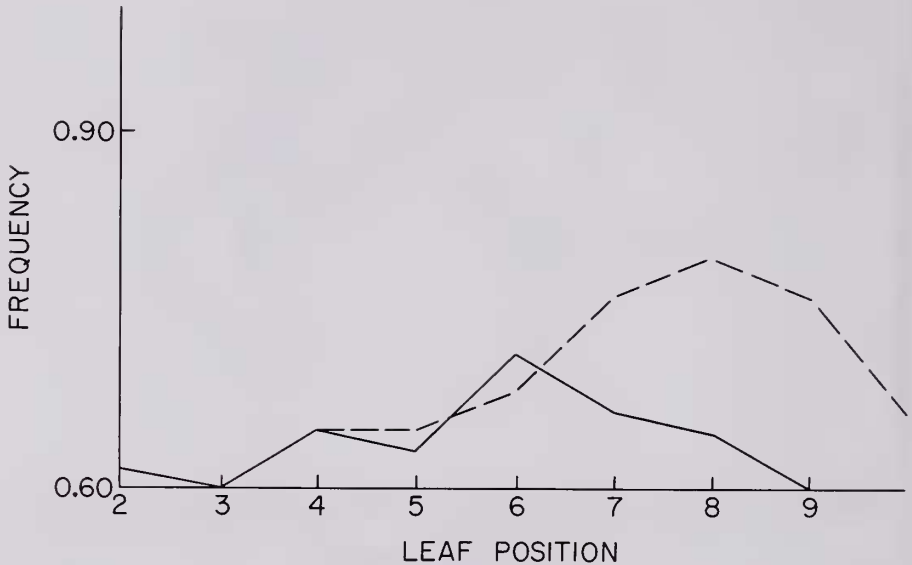


Fig. 6. Frequency polygons of elongate (solid line) and oblique (dashed line) gall positions for tree 1. Ordinate: frequency; Abscissa: leaf position.

1 are shown in Figure 6. The solid line shows the frequency distribution of the position of elongate galls, and the dashed line that of oblique galls. The mean gall positions of the two types differ for these shoots ($F_s = 12.3 > F_{.005(1,47)}$). It is apparent from a comparison of Figures 5 and 6 that both elongate and oblique galls are, on the average, in a position that should result in greater fitness for each. Also, although the figures do not show it, the last 1 or 2 leaves among the early leaves usually have smaller blades and petioles. The oblique and elongate galls, then, are usually on one of the leaf positions that have the greatest average leaf and petiole sizes, respectively.

Similar data are shown for tree 3 in Figures 7 and 8. Here, the positions of oblique and elongate galls are not significantly different (Figure 8). The mean positions are marked as crosses on the lines. The average petiole lengths at the peaks at positions 6 and 8 are also not significantly different ($P = .70$). Elongate and oblique galls again are near the optimal positions, but this time with more overlap between the two species. It may be that the timing of gall initiation of one or both species on tree 3 is slightly different from that of tree 1, but the observed difference in positions is better explained by a greater rate of early leaf expansion in tree 3, creating a higher mean position of each species and at the same time, less separation in position between the two.

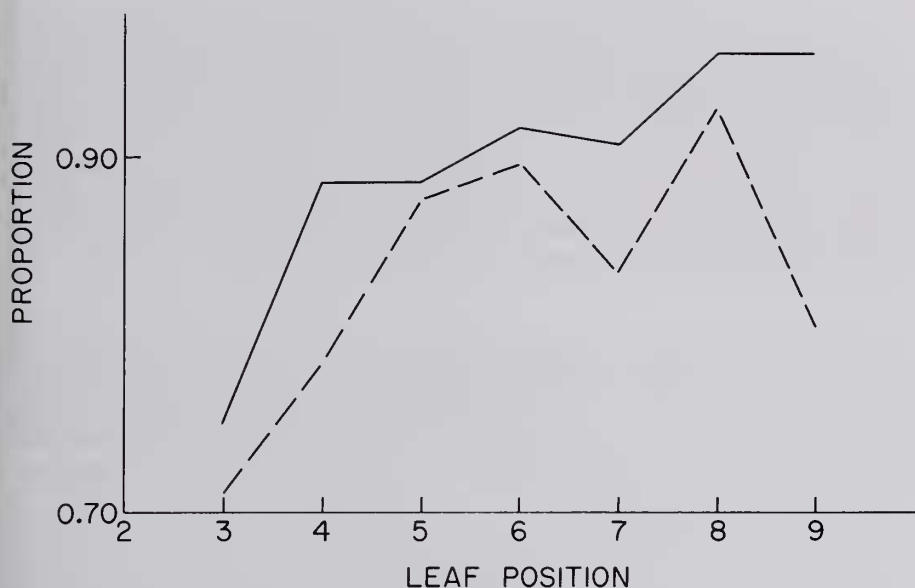


Fig. 7. Average proportion of maximum leaf length (solid line) and petiole length (dashed line) on leaf position. Ordinate: proportion of maximum length; Abscissa: leaf length. Data are for tree 3, Stony Brook, New York, 1975.

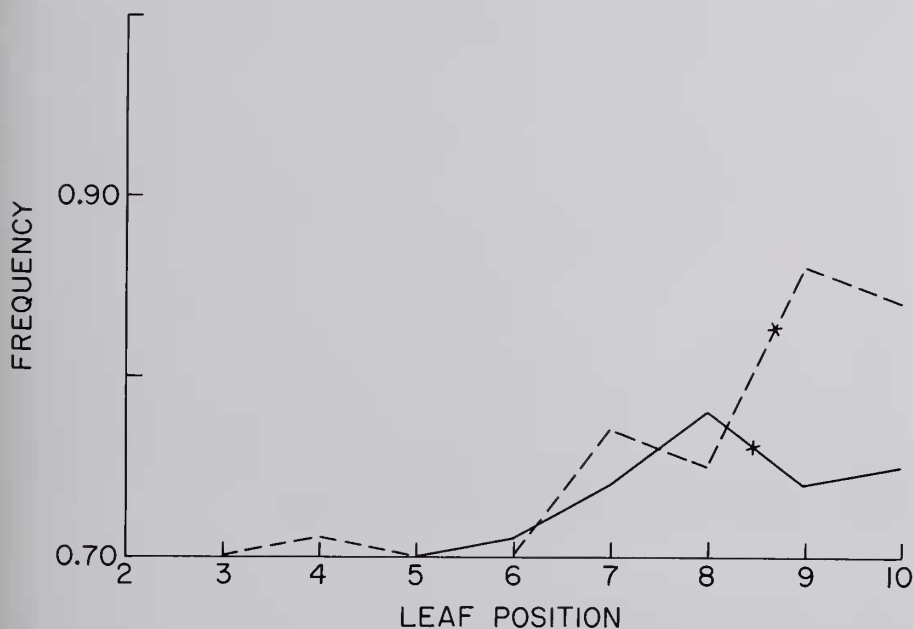


Fig. 8. Frequency polygons of elongate (solid line) and oblique (dashed line) gall positions. Ordinate: frequency; Abscissa: gall positions. Data from tree 3, Stony Brook, New York, 1975.

It appears that the average earlier timing of elongate galls relative to oblique galls may be a strategy to obtain longer petioles, thereby increasing population size. Similarly, oblique gall position seems to correspond to the largest leaf position among the early leaves. If trees had growth patterns similar to that of tree 1, later elongate gall initiation would be selected against. The earlier initiation of elongate galls relative to oblique galls may be a result of the growth pattern in which petiole length, on the average, reaches its peak before leaf length among the early leaves.

Summary

The aphid, *Pemphigus populitransversus*, producing galls on the petioles of cottonwoods, *Populus deltoides*, was shown to comprise two forms differing in time of gall initiation and resulting in galls on early leaves and late leaves of the shoots. This dimorphism in position corresponds to the elongate-globular dimorphism previously described for this species.

The factors determining population size in the galls of these two morphs were explored. In each case, gall length and width correlated strongly with population size. Length of the leaf bearing the gall showed no correlation with population size within each morph. However, leaf length did help account for differences in population size between the two morphs.

The greater population sizes of globular galls are related to their larger size relative to elongate galls. Globular galls were shown to be significantly greater in length, width, and depth measurements. Petiole size was shown to account for much of the variation in gall size in *P. populitransversus*, both among and within morphs. The larger petioles of the late leaves help account for the larger size of the globular galls; hence, the greater population sizes of globular galls is due, in part, to the strategy of late gall formation, through the indirect effect of petiole size on population size.

Within the late leaves, globular galls tended to be formed on leaves before those with maximal petioles. Among the early leaves, elongate galls did seem to be in an average position that matched the position of the longest petiole. The galls of *P. populicaulis* were in a position such that leaf size was nearly maximized. The dimensions of elongate galls were dependent more on petiole size and those of oblique galls more on leaf size. This agrees with their sites of gall formation. The tendency among early leaves for petiole size to reach a maximum before leaf size may explain the slightly earlier initiation of elongate compared to oblique galls.

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